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Clarifying a male color morph of *Sphaerodactylus macrolepis* Günther, 1859 and resolving the taxonomic confusion on Saint Croix

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Abstract

Many species of sphaerodactyl gecko exhibit sexual dichromatism. In particular, dichromatism plays an important role in intersexual signaling for *Sphaerodactylus*. Furthermore, some species exhibit polymorphism in male color and pattern. Here, we describe a regional male color morph of *Sphaerodactylus macrolepis* from St. Croix. After generating both mitochondrial and nuclear phylogenies, we found that individuals with the St. Croix-specific yellow/orange head morph are part of the S. macrolepis clade. This distinct color morph likely contributed to the turbulent taxonomic history of the *S. macrolepis* species group. Given the documented diversity of the color patterns in this group and that sexual signals evolve rapidly, we suggest *S. macrolepis* is an excellent group to study the ecological and evolutionary consequences of dichromatism and polymorphism.

Key words: dichromatism, gecko, sexual dimorphism, sphaerodactyl, Sphaerodactylidae, Virgin Islands

Introduction

Sphaerodactylus is a speciose lineage of miniaturized geckos distributed throughout the Caribbean, Central America, and northern South America (Barbour 1921; Schwartz 1973; Harris 1982; Harris & Kluge 1984; Schwartz & Henderson 1991). This lineage is well-known for its color and pattern diversity (e.g. Schwartz 1973; Padilla 2006; Thorpe *et al*. 2008; Daza *et al*. 2019; Yuan *et al*. 2020). Many *Sphaerodactylus* exhibit sexual dichromatism, with males tending to have light background color on their heads compared to the rest of their bodies (Schwartz 1965, 1973). In this case, male coloration is likely a long-distance visual signal for potential mates (Regalado 2012; Powell & Uy 2023).

Sexually dimorphic traits have played an important role in diagnosing new species of *Sphaerodactylus* (Thomas & Schwartz 1966a,b; Thomas & Hedges 1993). However, the existence of color and pattern polymorphism has led to some taxonomic confusion (Thomas & Schwartz 1966a; Daza *et al*. 2019; Yuan *et al*. 2020; Powell & Uy 2023). This is particularly evident in the taxonomic history of the big-scaled leaf-litter gecko (*Sphaerodactylus macrolepis*) and its allies from islands on the Puerto Rican bank. *Sphaerodactylus macrolepis* was originally described from St. Croix by Günther (1859). In the 164 years since its description, *S. macrolepis* has routinely been the subject of taxonomic revision, including description, synonymization, and resurrection with other Puerto Rican and Lesser Antillean forms such as *Sphaerodactylus grandisquamis*, *Sphaerodactylus monensis*, and *Sphaerodactylus parvus* (Stejneger 1904; Schmidt 1920; Barbour 1921; Grant 1931, 1932a,b,c; King 1962; Thomas & Schwartz 1966a). While diverse morphological traits were used to distinguish taxa, some taxonomic changes were heavily influenced by male coloration (Thomas & Schwartz 1966a).

The Virgin Island *S. macrolepis* were differentiated from geckos on Puerto Rico by Stejneger (1904), who named the Puerto Rican form *Sphaerodactylus grandisquamis*. However, *S. grandisquamis* and *S. macrolepis* were later synonymized (Barbour 1921; Schmidt 1920). Soon after, Grant (1931) described five new *Sphaerodactylus* species on Puerto Rico and nearby islands. Among these were a new form from Culebra, *Sphaerodactylus danforthi*, which was phenotypically very similar to *S. grandisquamis* and *S. macrolepis*. Grant (1932a) later revived *S. grandisquamis* and expanded the distribution of *S. danforthi* to include Vieques (Grant 1932b; Grant 1932c). Precise locality information was limited in all of these studies. For a time, there was stability with *S. macrolepis* in the Virgin Islands, *S. danforthi* on Culebra and Vieques, and *S. grandisquamis* on Puerto Rico (Barbour 1937; Heatwole *et al.* 1963). This arrangement was significantly altered by a monographic revision of the Puerto Rican *Sphaerodactylus* by Thomas and Schwartz (1966a), who synonymized *S. grandisquamis* and *S. danforthi* with *S. macrolepis* and erected subspecies to describe morphological differences among *S. macrolepis* populations in Puerto Rico and surrounding islands.

Thomas and Schwartz (1966a) recognized, very broadly, two groups in the *S. macrolepis* species complex. First, were geckos from the Virgin Islands, including St. Croix (now called *S. macrolepis*), distinguished by having multiple, microscopic hair-like structures on each dorsal scale. In the second group were geckos from Puerto Rico and Vieques (now called *S. grandisquamis* and *S. inigoi,* respectively), which, like the Virgin Islands form, had dorsal scales with multiple, microscopic hair-like structures, and, on the periphery of each scale, multiple knob-like structures. These differences ordinarily might have resulted in their separation into two distinct species. However, Thomas and Schwartz (1966a), like others before them (Grant 1932b), struggled to make sense of the Vieques geckos (*S. inigoi*), which appear, in many respects, intermediate between the Puerto Rican and Virgin Islands forms, saying, "... specimens from Vieques have the scale organs of *grandisquamis* but the pattern and coloration of *macrolepis*." While Thomas and Schwartz (1966a) do not explicitly mention the coloration of male *S. macrolepis* from St. Croix in this comparison, they describe *S. inigoi* males from Vieques having, "...head orange to rusty and without pattern..." and "a very few males from St. Croix have the head unmarked dorsally and more or less unicolor with the yellowish-brown body." Thus, it appears the existence of patternless, yellow/orange-headed males on both Vieques and St. Croix caused them to refrain from splitting up *S. macrolepis* s.l.

Subsequent molecular phylogenetic analyses (Daza *et al*. 2019) have clarified evolutionary relationships among these forms and their taxonomy resulted in elevation of *S. inigoi* from Vieques to species status. Phylogenetic analyses indicate *S. inigoi* and *S. grandisquamis* form a clade that is sister to a clade composed of *S. parvus* (from Anguilla, St. Barts, and nearby islands) and *S. macrolepis* from the Virgin Islands. The subspecies of *S. grandisquamis* exhibit a variety of head colorations in mature males, ranging from blue to bright yellow to orange background colors and various degrees of overlying dark brown blotches, reticulations or pixelations (Padilla 2006; Daza *et al*. 2019). Mature males of *S. inigoi* exhibit orange background color with little overlaying pattern (Daza *et al*. 2019). Mature males of *S. macrolepis* typically exhibit blue background color with various degrees of dark brown reticulate overlay (Fig. 1a; Daza *et al.* 2019). However, the presence of yellow-headed males without patterning on St. Croix remains to be thoroughly investigated. Are these yellow-headed geckos introduced from some nearby populations with yellow or orange heads (e.g. Puerto Rico, Culebra, Vieques, or other Virgin Islands)? Or are they *S. macrolepis*, representing a polymorphism on St. Croix? Herein, we aimed to use genetic data to confirm whether this yellow-headed male color morph on St. Croix is a polymorphism within the local population or the result of immigration from outside St. Croix.

Materials and Methods

We conducted field work in St. Croix, US Virgin Islands from 27 May 2021 to 2 June 2021 (Permit: DFW21009X to SVN). During this time, we collected eight individuals of *Sphaerodactylus macrolepis* (four males and four females) and putatively assigned sex as male or female via external morphological features: dichromatic coloration and/or escutcheon scale morphology (Grant 1931), while recognizing that sexual traits are multimodally distributed (McLaughlin et al. 2023). Upon discovering some males with patternless, orange head coloration (Fig. 1), we believed there may have been an introduction of *Sphaerodactylus inigoi* from nearby Puerto Rican islands (potentially the

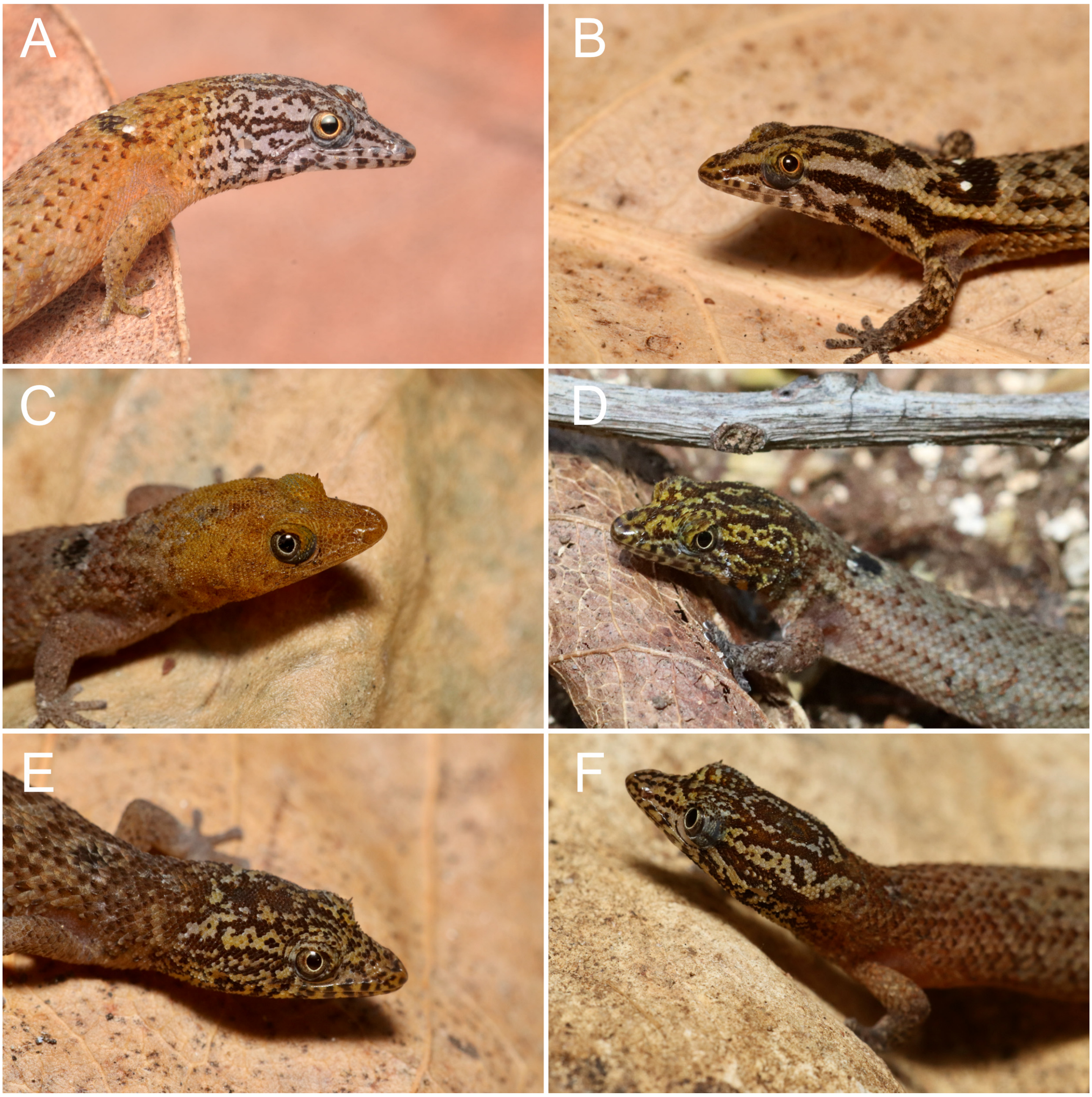

FIGURE 1. Variation in *Sphaerodactylus macrolepis* head coloration. (A) Male from Culebra, Puerto Rico exhibiting a blue head. (B) Female from St. Croix exhibiting typical background coloration on the head that matches the dorsum. (C) Male from St. Croix exhibiting an orange background color with no pattern. (D) Male from St. Croix exhibiting a bright yellow background color with vermiculate pattern. (E–F) Males from St. Croix exhibiting a dull yellow with some blue background color with vermiculate pattern.

most proximal islands, Vieques or Culebra; *sensu* Daza *et al.* 2019). To test this hypothesis, we constructed phylogenetic gene trees to determine whether the specimens with yellow/orange heads from St. Croix should be ascribed to the native *S. macrolepis* and not introduced *S. inigoi* (or, a third possibility, whether they are hybrids with another species of *Sphaerodactylus*). We PCR-amplified and Sanger-sequenced three individuals, AHG8 (male), AHG13 (male), and AHG25 (female) for the mitochondrial gene NADH dehydrogenase subunit 2 (ND2) and adjacent tRNAs, and the nuclear gene recombination-activating gene 1 (RAG1). Information of primers and PCR conditions are detailed in Gamble et al. (2008a,b, 2011, 2012). We obtained additional *Sphaerodactylus* samples from Genbank (MN415574-MN415765 and MN415766-MN415965; Daza et al., 2019). The additional St. Croix *S. macrolepis* samples from Daza et al. (2019) were ethanol-fixed. Males appeared to have typical gray heads, although yellow colorations could have disappeared due to storage conditions. The ND2 sequence for sample AHG25 was of poor quality and removed from further study. We assembled the sequences in Geneious (R9.1.6; Kearse *et al.* 2012) using MUSCLE (Edgar 2004) and inspected the resulting alignment by eye for errors. We used ModelFinder (Kalyaanamoorthy *et al.* 2017) to test alternative partition schemes and models of evolution using the Bayesian information criterion, then generated maximum likelihood gene trees using IQ-TREE (v2.1.2; Nguyen *et al.* 2015) with the selected models. We estimated nodal support using 1000 ultrafast bootstrap approximations (UFBoot; Hoang *et al*. 2018). To further investigate color morphs of *S. macrolepis*, we searched "Research Grade" observations in the Virgin Islands on iNaturalist (iNaturalist 2023).

Results

We did not find any blue-head morphs of *S. macrolepis* during our field work on St. Croix (Fig.1a), although blue-head morphs are documented on the island (photograph by Toby Hibbits, Daza et al. 2019). Females exhibited typical color patterns of yellow-tan background along the entire body with a dark brown, striped, overlaying pattern on the head (Fig. 1b). Some male individuals we observed exhibited orange, unpatterned heads (Fig. 1c), some with bright yellow heads with reticulate dark brown patterns (Fig. 1d), and many with dull yellow-grey heads with reticulate dark brown patterns (Fig. 1e–f). We recovered the orange- and yellow-head males embedded in clades of *S. macrolepis* in both the ND2 and RAG1 phylogenies (Fig. 2; Supplemental Material 1,2) with high support for the ND2 tree and moderate support for the RAG1 tree. Upon investigating iNaturalist, we found that all *S. macrolepis* reported from St. Croix exhibited either the typical juvenile/female coloration or a spectrum of the yellow- to yellow-grey-head morphs (iNaturalist 2023). Observations from the remaining islands of the United States Virgin Islands and British Virgin Islands exhibited either the typical juvenile/female coloration or the blue-head morph (iNaturalist 2023).

Discussion

We report a novel color morph of male *S. macrolepis* from St. Croix that appears distinct from other islands in this species' range and demonstrate that the distinct orange- and yellow-head color morphs of *Sphaerodactylus macrolepis* are common on St. Croix (Fig. 1). The recovery of these morphs in clades of *S. macrolepis* for both ND2 and RAG1 suggest that these are indeed *S. macrolepis*. There is no support for alternative hypotheses that an introduction of *Sphaerodactylus inigoi* or hybridization between two *Sphaerodactylus* species occurred (Fig. 2; Supplemental Material 1,2). MacLean (1982) noted that males of *S. macrolepis* exhibited "bright orange" or "red" heads on "some islands" but with no explicit locality information. Our findings mirror patterns of sexual dichromatism seen in the mainland species *S. grandisquamis*, in which different subspecies exhibit distinct male coloration, including blue, red, and yellow heads (Daza et al. 2019). Further work may focus on confirming whether the yellow-head morph of *S. macrolepis* is island-wide or allopatric with the blue-head morphs.

The presence of this color morph likely contributed to the turbulent taxonomy of Puerto Rican *Sphaerodactylus* (Grant 1931; Thomas & Schwartz 1966a). Early work on *Sphaerodactylus* from St. Croix failed to mention head color of males (Günther 1859; Barbour 1915). Grant (1931) described *Sphaerodactylus danforthi* as a species from Culebra, overall morphologically similar to *S. macrolepis sensu lato*, and exhibiting both a speckled blue-head male morph and a "red"-head male morph. Grant (1932b) later reported this species from Vieques and St. Croix (Fig. 3; Grant & Beatty 1944). *Sphaerodactylus danforthi* has since been synonymized with *S. macrolepis* (Thomas & Schwartz 1966a; Daza *et al*. 2019). We now know that the "red"- head morphs of *S. danforthi* from Culebra and Vieques were *S. inigoi* (Daza *et al.* 2019), and we can safely assume those described from St. Croix by Grant & Beatty (1994) are the yellow-/orange-head morph *S. macrolepis sensu stricto*. We can also clarify that similarities in male head coloration between *S. inigoi* from Vieques and *S. macrolepis* s.s. reported by Thomas & Schwartz (1966a) are due to convergence.

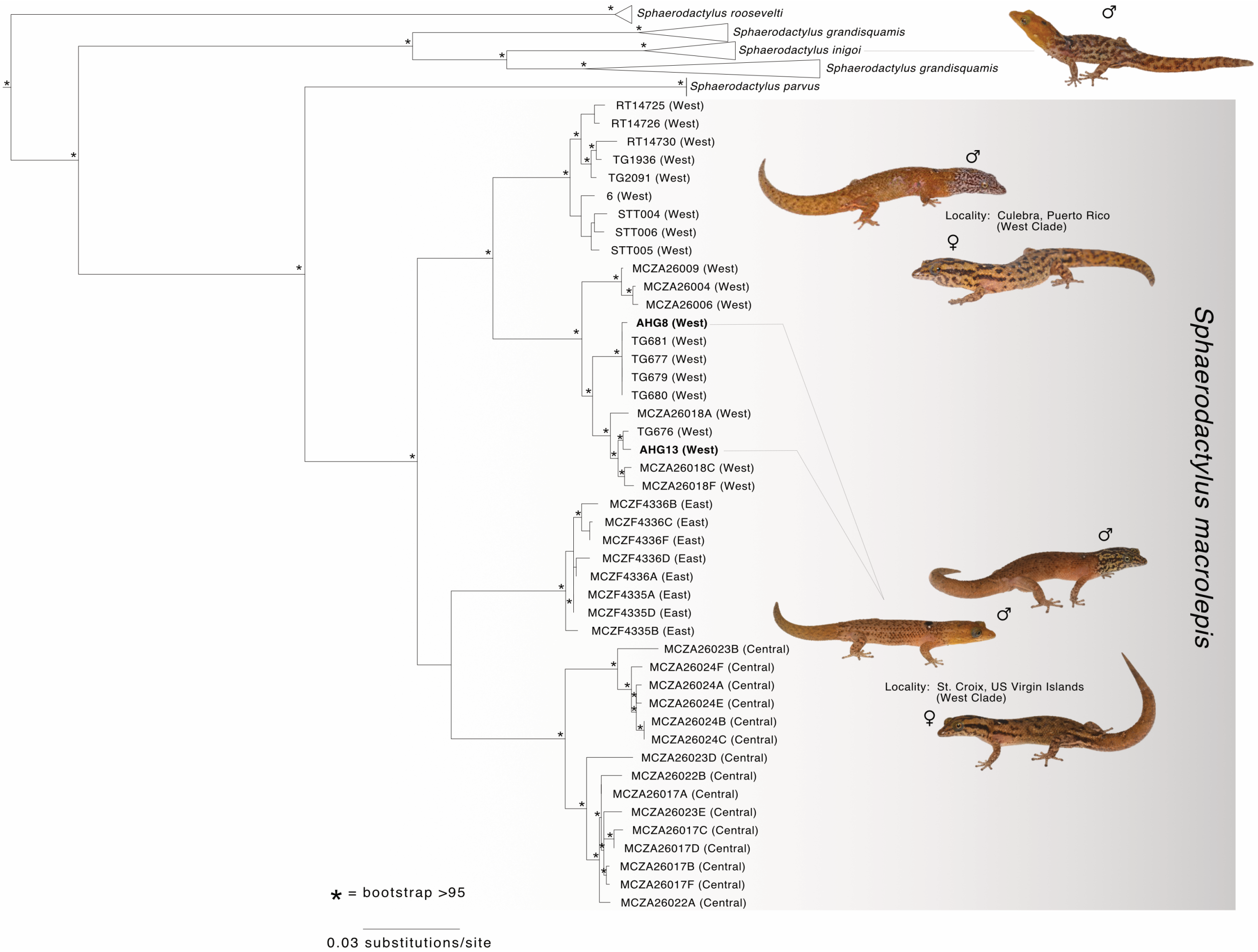

FIGURE 2. Maximum likelihood phylogeny of *Sphaerodactylus macrolepis* ND2 demonstrating that field-collected "yellow/ orange head" morphs from St. Croix (AHG008, AHG013) are embedded within the *S. macrolepis* clade and not *S. inigoi*. The West clade composed of individuals from southern Culebra (Puerto Rico), St. Thomas and St. Croix (US Virgin Islands), and Jost Van Dyke and Little Thatch Islands (British Virgin Islands). The East clade is composed of individuals from Necker and Moskito Islands (British Virgin Islands). The Central clade is composed of individuals from Cooper, Salt, Beef, and Guana Islands (British Virgin Islands; Daza et al. 2019). Asterisks represent nodes with high support (>95 bootstrap value).

Sexual dichromatism and color polymorphisms play important roles in communication and mate recognition, both of which impact speciation and evolution. Polymorphisms can lead to markedly different behaviors not limited to mate choice (e.g. Brock & Madden 2022), sometimes related to physiologies (e.g. Sinervo *et al*. 2000), and potentially prime a lineage for reproductive isolation and ultimately speciation (e.g. Gray & McKinnon 2007). Sexual signals, such as dichromatism, can evolve rapidly and are important components of *Sphaerodactylus* communication (Regalado 2012, 2014; Martin & Mendelson 2014; Hemingson *et al.* 2019; Powell & Uy 2023). Further, male polymorphisms in dichromatic *Sphaerodactylus* species can affect mate recognition (Powell & Uy 2023). The putative species-level variation among *S. macrolepis* populations observed by Daza *et al.* (2019), in tandem with the unique color polymorphism we describe here and the geographic distance from other islands, suggests the St. Croix population is in the process of reproductive isolation. Future work on this system should include extensive genetic sampling and behavioral experiments between *S. macrolepis* populations across its distribution. *Sphaerodactylus macrolepis* may serve as an excellent model to study the downstream evolutionary and ecological processes color polymorphisms affect. Finally, taxonomists should be cautious using male color and pattern as a diagnostic character given the frequency with which the similar dichromatic traits arise among independent *Sphaerodactylus* lineages.

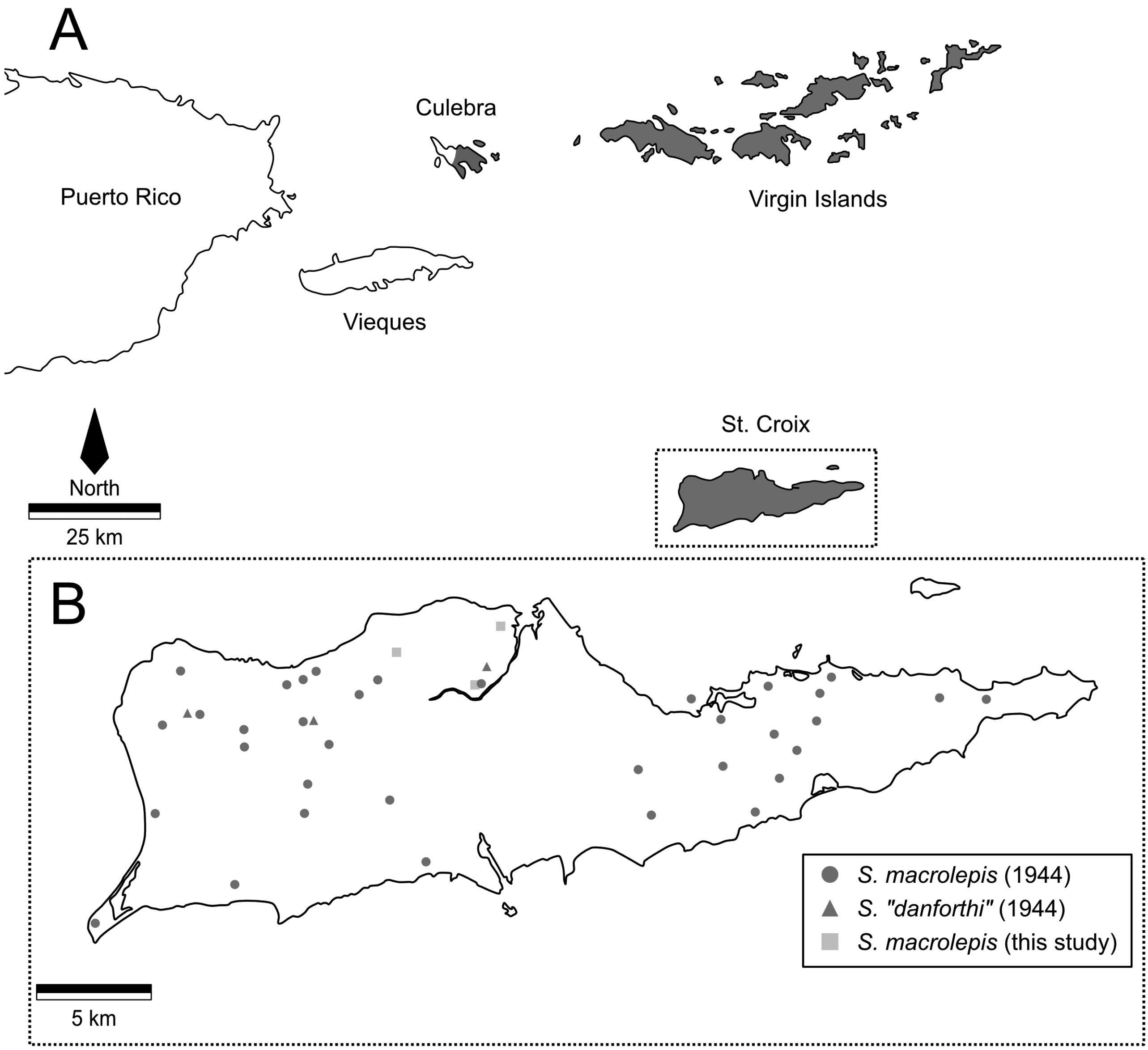

FIGURE 3. (A) Map of eastern Puerto Rican islands and the Virgin Islands. Gray illustrates the range of *Sphaerodactylus macrolepis sensu stricto* (Daza et al., 2019). (B) Map of St. Croix depicting *S. macrolepis* and *Sphaerodactylus "danforthi"* samples noted by Grant and Beatty (1944; gray circles and triangles) and those collected for this study (orange squares).

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